Reference: *Biol. Bull.*, **136**: 469–482. (June, 1969)

INTERTIDAL ZONE-FORMATION IN *POMATOLEIOS KRAUSSII* (ANNELIDA: POLYCHAETA)[1]

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Pomatoleios kraussii forms a well-defined intertidal zone in many areas of its Indo-Pacific distribution (for details of this distribution see Straughan, 1967a). However, Straughan (1968) noted that this species settles and survives subtidally, and in artificial habitats (for example water cooling systems) that are continually submerged. Hence the intertidal distribution of *Pomatoleios* is not the result of differential larval settlement. The following study was designed to determine the factors contributing to the formation of an intertidal zone by *Pomatoleios* in Hawaii.

Physiography

Coconut Island is situated in Kaneohe Bay on the northeastern (windward) coast of the island of Oahu (21°26′N, 157°48′W). It is a small, partially artificial island surrounded by a reef flat of mainly dead coral. Experimental studies were conducted on the protected side of the island—furthest from the open sea.

Temperature

Over a one year period, May 1967 to May 1968, surface water temperatures varied between 19° and 28° C, and remained above 25° C from May to October (Bathen, 1968).

Salinity

A number of streams discharge into Kaneohe Bay. During wet winter months, and particularly following heavy rain, the bay fauna is exposed to salinities somewhat lower than normal seawater. Bathen (1968) reported salinities of 35 to 36‰ for eight months of the year with a minimum salinity of 31‰ in November.

Water movement

Surface currents across the reef and inshore of the island are dependent on tide and wind. Bathen (1968) reported that the north-northeast Trade Winds increase surface currents on rising tides and decrease currents on falling tides; whereas the southern Kona Winds (November through April) may have the reverse effect. The tides are mixed but the days on which there is only one tide are limited to two or three a month.

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Northeast Trade Waves (4 to 12 feet high) enter Kanehoe Bay for 90 to 95% of the time during summer and 55 to 60% of the time during winter. At other times during winter, the North Pacific Swell (8 to 14 feet high) predominates (Moberly and Chamberlain, 1964). During the present study, the latter commenced to influence the effective sea level on September 17 when the surf level rose on the north shore of Oahu (Dr. Jeannette Whipple Struhsaker, personal communication). Although this effect is damped in the Bay, a rise in effective sea-level is still evident during October. The theoretical Mean Sea Level is 1.0 to 1.2 feet above Datum.

Material and Methods

Temperature

Recorded by continually exposed maximum-minimum thermometers (accurate to 0.2° C) placed at the same level as intertidal populations of *Pomatoleios* on both the eastern and western sides of Stations C and G. Hence they recorded both water and air temperatures to which the population was exposed.

Salinity

Measured periodically with a refractometer accurate to 0.5‰.

Water movement

Surface water currents were gauged timing floats over measured distances, under calm conditions, at midflood and midebb of the tide when the tidal ranges were 1.6 feet and 1.8 feet, respectively. Measurements were made at inshore and reef flat stations.

Distribution and abundance of Pomatoleios

A. Distribution around the coast of Oahu: In June and July the following localities were surveyed for *Pomatoleios*: Kahuka, Koko Head, Black Point, Kewalo Basin, Nanakuli, and Maille Point, as well as Coconut Island. These localities were selected as being representative of all types of intertidal habitats found on Oahu.

B. Distribution and abundance across the Coconut Island Reef: Seven Stations A through G were selected along a straight line transect from the shore (Station A) to the reef edge (Station G). The density of *Pomatoleios* was estimated from direct counts of tubes at each station. Separate estimates were made for the eastern (facing flood tidal current) and western (facing ebb tidal current) sides of each station. Two inch I beam steel stakes at Stations C, F, and G provided suitable substrate extending beyond the normal vertical range of *Pomatoleios* in both directions. At Station A the cement wall extended above this range only. The available surfaces on coral boulders at Stations B, D, and E were entirely within this range. At the same time, the abundance of the barnacle *Balanus hawaiiensis* Brock; the oysters *Ostrea sandvichensis* Sowerby and *O. gigas* (Thunberg); vermetid molluscs, the ascidians *Didemnun candidum* Savigny, *Trididemnun profundum* (Sluiter), *Symplegma* sp., *Botrilloides* sp.; and algae were recorded at all stations. The initial survey was made between June 24 and 28 and the final survey was made on October 21.

Larval settlement

Fouling plates (80 × 100 mm) mounted vertically at intervals of 1.5 inches, 12 to a frame, were placed at an inshore Station C and reef edge Station G two or 14 days before predicted larval settlement. (For details of the frame structure see Straughan, 1967b). The following types of plates and corresponding surfaces were mounted in two duplicated series per frame.

Clear glass		smooth, light, transparent
Ground glass		rough, dark, transparent
Black smooth glass		smooth, dark, transparent
Black smooth glass		rough, dark, transparent
Black bakelite (used as standard Plate)		smooth, dark, opaque
Asbestos cement	Side 1	smooth, light, opaque
	Side 2	pitted, light, opaque

Standard black bakelite plates mounted at an angle of 60° to horizontal were placed at both Stations two days before predicted settlement.

At Station C, 12 standard black bakelite plates were mounted horizontally 1.5 inches apart with the uppermost plate 11 inches above datum. This series was examined every 14 days from July 9 to October 25. On October 1 a second series of 12 plates was added 1.5 inches above the original series.

Spacing within populations of different densities was examined using distance to nearest neighbor as a measure of spatial relationships after the method of Clark and Evans (1954). The ratio (R) of observed mean distance between points of a population to the expected mean distance between points of a randomly distributed population serves as a measure of departure from randomness. In a random distribution, $R = 1$. Under conditions of maximum aggregation $R = 0$. Under conditions of maximum spacing $R = 2.1491$.

Survival

At low salinities: 50 adult specimens of *Pomatoleios* were placed in 2 gallon aquaria containing aerated water of salinities of 0‰ and 31‰ for varying periods before being returned gradually to seawater. The number of surviving animals was counted after 1 hour in seawater (salinity 35.5‰).

Under conditions of sand accumulation: 16 equal populations of established juvenile *Pomatoleios* were placed so that half were in positions free of sand and half in positions of sand accumulation. Survival in both series was determined after 14 days.

At high intertidal levels: In July established populations of 65 and 63 adult *Pomatoleios* were placed above the level of the *Pomatoleios* zone at Stations G (reef edge) and C (inshore) respectively, so that they were above the upper limit of settlement for that month but within the range of October settlement. Equal populations of adult *Pomatoleios* within the settlement range for July were used as controls. In all cases 50% of the population was on upper surfaces.

With "competition for space": The Spearman rank correlation coefficient

(Seigel, 1956) was used to show any association between the relative abundances of compound ascidians and *Pomatoleios*. The percentage of each fouling plate covered by compound ascidians per 14 days was compared with the survival of *Pomatoleios* on that surface.

Results and Observations

Distribution and abundance of Pomatoleios

A. Distribution around the coast of Oahu: Although many of the 12 species of the sub-family Serpulinae recorded from Oahu, were widely distributed around the island, *Pomatoleios* was found only in sheltered areas within Kaneohe Bay. The other localities visited were on the open coast and exposed to wave and surf action. *Pomatoleios* may also occur in Pearl Harbor where sheltered conditions similar to those in Kaneohe Bay exist. This area was not surveyed because of United States Navy restrictions. However, the high level of pollution in the Harbor may exclude *Pomatoleios*.

B. Distribution and abundance across the Coconut Island Reef in Kaneohe Bay: The following physical factors might contribute to limiting distribution and

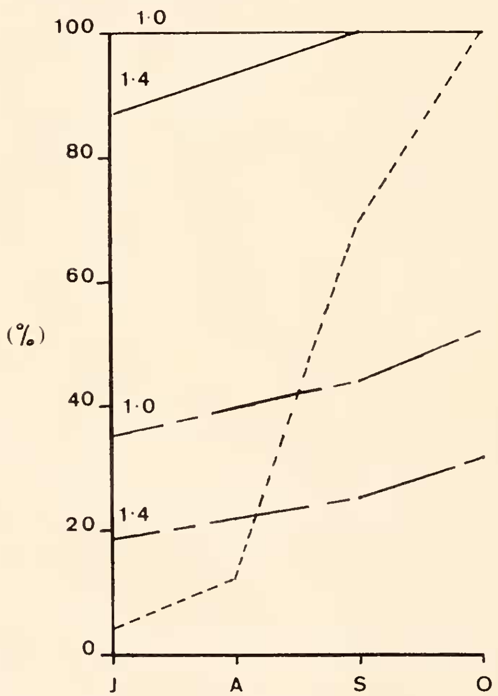

FIGURE 1. ———— = predicted percentage of days that 1.0 and 1.4 foot levels were submerged for part of the day; — ——— — = predicted percentage of hours that each level was submerged; — — — — = percentage of *Pomatoleios* settling on top 4 plates (= *Pomatoleios* zone) of the original 12 plate series, from July to October inclusive. Predictions were made from Tide Tables.

abundance of *Pomatoleios;* 1. Frequency and period of submergence, 2. Water movement, 3. Salinity, and 4. Temperature.

If other effects are ignored, the frequency and duration of submergence of a given level above datum can be predicted from tide tables. There is a gradual increase in the predicted frequency of submergence of the 1.0 foot and 1.4 foot levels from July to October (Figure 1). In July, the level of minimum High Water Spring (Min.H.W.S.) (that is, the highest level that is submerged every day) is 1.0 feet, while in September and October it is 1.4 feet. That is, in October, the predicted frequency that the 1.4 foot level is submerged equals that predicted for the 1.0 level in July, *i.e.*, once a day.

In July, the 1.0 foot level should be submerged 35% of the time, while in October, the 1.4 foot level should be submerged 31% of the time. On calm days during October, the tide remained above the predicted level although the tides approximated closely the predicted level in July. The rise in effective sea level was sufficient to increase the predicted time of submergence of 1.4 foot level in October to approximately that of the 1.0 foot level in July. This change most markedly affected larval settlement but also was responsible for changes in abundance.

Tidal current velocities inshore were 0.083–0.125 meters per second east to west on the flood tide, and 0.0415 meters per second west to east on the ebb tide. Current velocities on the reef flat were 0.25–0.3 meters per second east to west on flood tide and 0.09 meters per second west to east on the ebb tide. Therefore reef flat stations were exposed to currents of 2 to 3 times the velocity of those at inshore stations. Since the inshore stations are more sheltered from the north-northeast Trade Winds, the expected difference in current velocities would be greater during periods of trade wind influence. The eastward side of objects is always exposed to currents moving at a higher velocity than is the westward side.

Salinity remained close to that of normal seawater (35–36‰) throughout the survey except following heavy rain on September 1 and October 1. On each occasion salinity dropped to 31.5‰ on the surface at Station C for no longer than 24 hours. No resulting mortality was observed and experiments showed that adult specimens of *Pomatoleios* can survive at least 17 hours in freshwater (0‰) and 30 hours at a salinity of 31‰.

Temperatures were recorded on both the eastern and western sides of inshore Station C and reef edge Station G. A temperature range of 23 to 30° was recorded within the intertidal range of *Pomatoleios* at all sites. Therefore, animals exposed to the afternoon sun (western side) were subjected to similar upper temperature extremes as those exposed to the morning sun (eastern side). Inshore Station C is possibly exposed to higher water temperatures than the reef edge Station G because water flows over shallow reef flat areas before reaching C, while it flows from deeper areas to G.

While *Pomatoleios* was recorded at each of Stations A to G in June, the population was more abundant at Station C (12.0/sq inch) than at the other stations (Table I). At Station C, it occurred from 4 inches below datum to 11 inches above datum and at the top of this range formed a zone 4 to 5 inches wide.

Pomatoleios occurred up to a higher intertidal level and was more abundant at inshore Stations (A and C) than at reef flat or reef edge Stations (F and G) (Table I). At Station C, *Pomatoleios* extends to a higher level on the western side (11 inches above datum) which is exposed to low velocity water currents, than the eastern side (9.5 inches above datum) which is exposed to high velocity water currents. At Station B, *Pomatoleios* was more abundant on surfaces

TABLE I

Details of distribution and abundance of Pomatoleios *and general distribution and abundance of other organisms at Stations A to G*

Station	Range in inches	Individuals per square inch	Algae	*Balanus*	*Ostrea*	Vermetid	Ascidian
Station A (concrete wall)							
SIP	−2.0 to 15.0	2.5					
Station B (rusting drum)							
EIP	−4.0 to 1.5	0.625	XX				
WIP	−4.0 to 4.5	0.925	X				
EIP	−2.0 to 3.5*	0.725	XX				
WIP	−1.0 to 4.0	1.0	X				
Station C (iron stake)							
EIP	above 9.5	0.0		X	X		
	5.5 to 9.5	12.0		X			
	0.0 to 5.5	0.24	X	X	X	X	
	−4.0 to 0.0	0.125	XX				
WIP	above 11.0	0.0		X	X		
	6.0 to 11.0	7.0		X			
	0.0 to 6.0	0.24	X		X	X	X
	−4.0 to 0.0	0.125	XX				
Station D (dead coral boulder)							
EFU	0.0 to 5.0	0.375			X		
WFL	0.0 to 5.0	0.25	XX				
Station E (dead coral boulder)							
EFL	0.0 to 3.0	0.75		X		X	
EFU	0.0 to 3.0	0.5		X		X	
WFU	0.0 to 3.0	0.25	X	X		X	
Station F (iron stake)							
EFP	above 5.0	0.0		XX			
	2.0 to 5.0	0.5		XX			
WFP	above 5.0	0.0		XX			
	2.0 to 5.0	0.25	XX				
Station G (iron stake)							
ERP	above 6.5	0.0		X	X		
	−2.0 to 6.5	0.06		XX			
WRP	above 6.5	0.0		X	X		
	−2.0 to 6.5	0.0		XX			

S—surface facing south F—reef flat station L—lower surface
E—surface facing east R—reef edge station X—present on surface
W—surface facing west U—upper surface XX—dominant on surface
I—inshore station P—perpendicular surface *—sheltered by other side of drum

sheltered from water currents than on those exposed to water currents. That is, *Pomatoleios* is most abundant and extends to the highest intertidal levels at sites that are exposed to low water currents.

At Station A, *Pomatoleios* occurred from 2 inches below datum to 10 inches above datum on smooth surfaces, and to 15 inches above datum on creviced surfaces. Further at Station D, a coral boulder entirely within the *Pomatoleios* range, *Pomatoleios* occurred in crevices and not on outer surfaces. In the latter case, shelter from sand abrasion as well as shelter from water currents is probably a limiting factor.

At E where the boulder had relatively flat surfaces, in the absence of sand, *Pomatoleios* was more abundant on a lower surface than on an upper surface. Both surfaces faced the same direction and bore similar densities of other species. On the western surface where sand as well as algae occurred, *Pomatoleios* was less abundant than on the eastern surface.

At Station A, although *Pomatoleios* was not abundant (density 2.5 per sq inch), it was the dominant sedentary species throughout its range. At Station C below the *Pomatoleios* zone but above datum, algae, *Balanus, Ostrea,* vermetids, and compound ascidians were common, while below datum, algae was abundant. There is an increase in *Balanus* abundance from the inshore Station C to the reef flat Station F and the reef edge Station G. At Stations B, C, D, E, F, the density of *Pomatoleios* decreases where the algal abundance increases. Therefore, water currents, sand, and algae probably effect the distribution and abundance of *Pomatoleios*.

In October, the only change in the distribution of *Pomatoleios* was its presence (density = 0.25 per sq inch) in a band 5 inches wide above the *Pomatoleios* zone at Station C. At Stations C, F, G, compound ascidians were abundant up to 5 inches above datum while algae (predominantly a species of *Ulva*) formed a zone 5 inches wide above this. The abundance of algae at Stations B, D, and E also had increased. Hence at C the compound ascidians now extended to the bottom of the *Pomatoleios* zone while the algae extended over the *Pomatoleios* zone. Therefore, the rise in effective sea level between July and October, is reflected in the rise in the intertidal distribution of *Pomatoleios,* compound ascidians, and algae.

Larval settlement

Pomatoleios larvae settled during periods of spring tides throughout the study. Larval settlement was abundant during July, almost ceased during August and increased again during September and October. Unpublished data from other areas indicates that breeding ceases during the winter months at water temperatures of 23° C and below. There was a green algal bloom in the study area co-incident with the August reduction in larval settlement. At this time, few *Pomatoleios* adults in the study area contained mature genital products, while those kept in the laboratory contained mature genital products.

Sand accumulated rapidly and algae grew quickly on newly exposed surfaces. Therefore, to compare larval settlement on different types of surfaces, the surfaces were exposed within a few days of predicted larval settlement while to study the effects of sand and/or algae on larval settlement, surfaces were exposed 14 days before predicted larval settlement.

Larval settlement of *Pomatoleios* on horizontal fouling plates (Station C, July 9 to August 6) is shown in Figure 2. Larval settlement was more abundant below the *Pomatoleios* zone (= top four plates of July) than within this zone and extended below the lowest level of living *Pomatoleios*. In October, larvae settled on plates from 0.5 to 1.4 feet above datum. That is, in July the larval settlement range extended below the adult survival range while in October the larval settlement range extended above the adult survival range. This rise in larval settlement range parallels the rise in effective sea level between July and October.

Figure 1 shows that there was a gradual increase in the percentage of larvae settling within the *Pomatoleios* zone from July to October. The biggest increase in percentage of larvae settling within the *Pomatoleios* zone occurred in September. In September, the percentage of days that the *Pomatoleios* zone was submerged, rose to 100%. This suggests that frequency of submergence is more important than

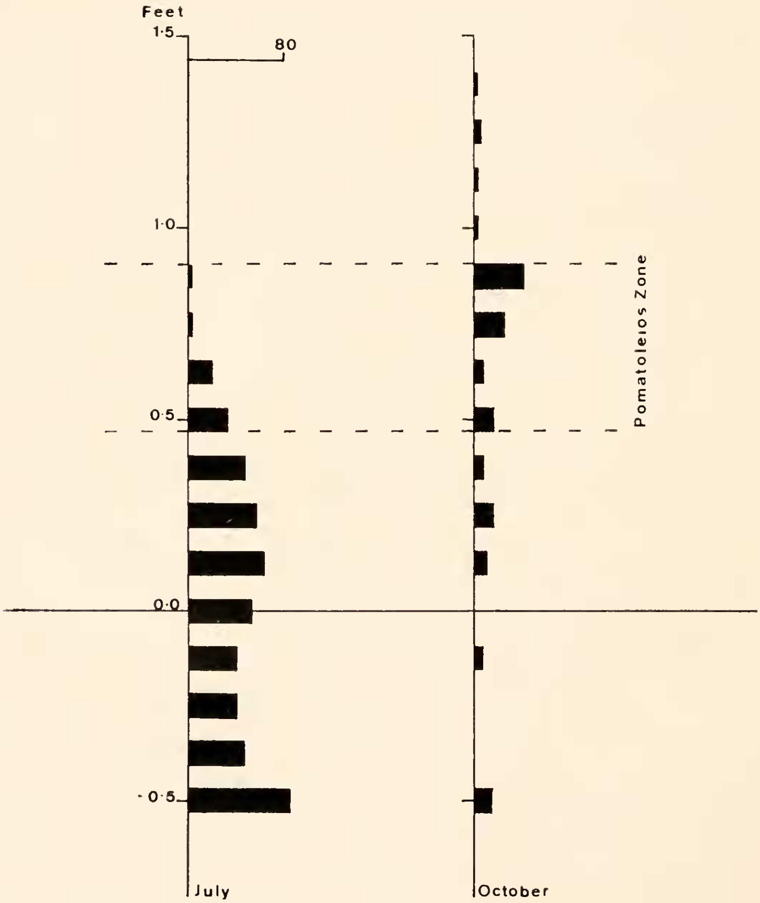

FIGURE 2. *Pomatoleios* settlement on 12 plates placed at the heights indicated during July. Number *Pomatoleios* on the above plates at the end of October and settlement on fouling plates placed above them during October.

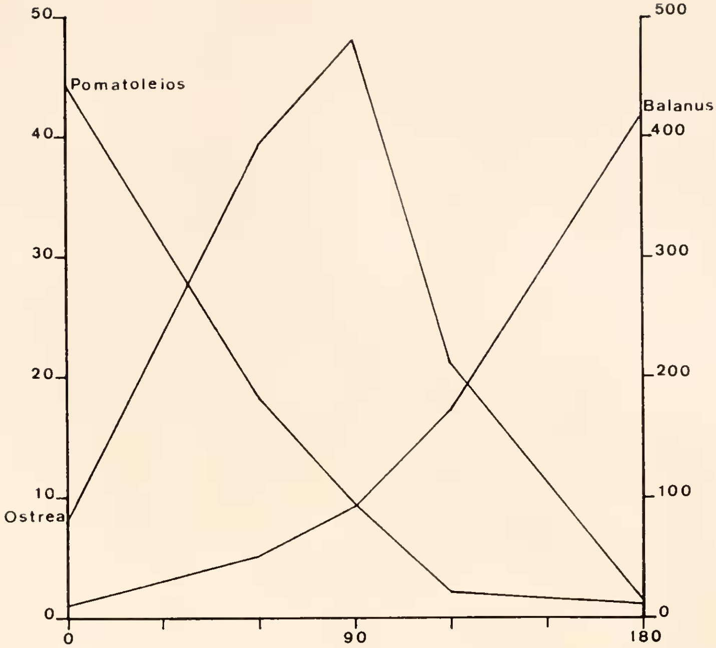

FIGURE 3. Number of larvae settling on fouling plates exposed at different angles. (0°–under surface; 90°–perpendicular; 180°–upper surface). *Pomatoleios* and *Ostrea* are plotted on the lower scale and *Balanus* on the higher scale.

overall percentage of time submerged in limiting the upper level of larval settlement.

Pomatoleios larvae did not settle evenly over the surface of fouling plates. In low density populations (density = 0.35 ± 0.03 per sq cm), individuals were randomly spaced (R = 0.93;0.88), while in higher density populations (density 0.6 per sq cm), they were aggregated (R = 0.417).

At Station A, larval settlement extended to a higher level on rough concrete than on smooth concrete. At Station C, experiments using fouling plates with different types of surfaces showed that larval settlement was also more abundant on a rough surface than on a smooth surface, and on a dark surface than on a light surface (Table II). Settlement on an evenly pitted surface did not differ from

TABLE II

Density (x per sq cm) Pomatoleios *settlement on different types of surface*

	Light transparent	Light opaque	Dark transparent	Dark opaque
Smooth	0.125–0.25	0.375	0.375	1.125–1.625
Evenly pitted		0.375		
Rough	0.5		2.0	

settlement on a smooth surface. Of the surfaces tested, larvae settled most abundantly on a dark, rough, transparent surface. However, this type of surface was not compared with a dark, rough, opaque surface which is probably even more suitable for larval settlement.

In Figure 3, larval settlement on fouling plates exposed at different angles at the same height above datum, is compared. *Pomatolcios* settlement was most abundant on the underside of objects (0°), and decreased with increasing angle until hardly any settlement occurred on the upper surface of objects. Of the other common intertidal species that may compete with *Pomatolcios, Balanus* larvae settled most abundantly on the upper surfaces (180°) and settlement decreased with decreasing surface angle. *Ostrca* larvae settled most abundantly on vertical surfaces but settlement was more abundant on the lower than the upper surfaces.

Table III

Number of larvae settling on fouling plates

Species	Reef edge		Inshore	
	Exposed	Sheltered	Exposed	Sheltered
Pomatoleios	0	0	0	12
	0	0	0	9
	0	0	0	13
	0	0	0	14
Balanus	56	25	0	0
	105	77	0	0
	104	48	8	0
	60	17	0	0
Ostrea	43	20	8	0
	84	46	0	0
	21	15	5	0
	16	9	0	0

Comparison of settlement of *Pomatolcios, Balanus,* and *Ostrea* on vertical fouling plates under conditions exposed to and sheltered from water currents at Station C (inshore) and Station G (reef edge) is made in Table III. *Pomatoleios* larvae settled more abundantly on inshore than reef edge fouling plates, and more abundantly on sheltered than exposed surfaces. In contrast, *Balanus* and *Ostrea* larvae settled more abundantly on reef edge than inshore fouling plates, and more abundantly on exposed than on sheltered surfaces. Therefore, there appears to be very little, if any, competition for space during larval settlement between *Pomatoleios* and *Balanus* and *Ostrea* larvae.

It is difficult to separate the effect of some physical factors on larval settlement, for example, current velocity and sand, and current velocity and presence of an algal mat. The latter at two weeks is composed of short algal species which trap some sand, and has a maximum thickness of 0.5 mm. In Table IV, the density of larval settlement under these varying conditions is tabulated. Situations where algae was absent and where sand was common, were always sheltered from the current, that is, alternatives "a" and "a_1" did not exist. No settlement occurred in high current velocity conditions, while under low velocity conditions, settlement was more abundant in the absence than presence of sand and the algal mat.

Survival

It was noted in the initial survey in July, that the adult population is more abundant in the absence than presence of sand and/or algae, and (above) that larval settlement is similarly effected. When sand accumulated after larval settlement a 25% mortality was recorded in six weeks. However, when established juveniles that settled in positions sheltered from sand, were placed in positions where sand accumulated, the mortality in two weeks was greater than that recorded among specimens that settled on the sandy side. Mortality also increased with the increasing accumulation of sand. (Thin layer of sand—25–37% mortality; 0.5 mm sand layer—34% mortality; 1.0 mm sand layer—56% mortality.)

TABLE IV

Density (x per sq cm) Pomatoleios *settlement on fouling plates exposed to currents of high and low velocities, in presence and absence of sand and algal mat*

Current	Sand		Algal mat	
	Absent	Present*	Absent	Present
High velocity	0.0	a	a_1	0.0
Low velocity	1.625	0.25	1.25–3.75	0.0

* 0.5 mm thick in 2 weeks.
Conditions represented by a, a_1 did not exist.

While the upper limit of larval settlement in July was the top of the *Pomatoleios* zone, it was possible that the more tolerant adults could survive at a higher intertidal level. However, when specimens were placed above the *Pomatoleios* range, at the reef edge (Station G), all (65) were destroyed by crabs in four weeks. Inshore (Station C), crabs destroyed 20% of the specimens above the *Pomatoleios* range but none within the *Pomatoleios* range. At the higher level, none of the remaining tubes on the upper surfaces contained living specimens of *Pomatoleios,* while 50% of the tubes on the lower surfaces contained living specimens of *Pomatoleios.* There was a 95% survival of specimens on upper and lower surfaces within the *Pomatoleios* zone. At these mortality rates, *Pomatoleios* could not survive above the *Pomatoleios* zone over the summer months. That is, larvae settling above the *Pomatoleios* zone at C during October, could not survive the following summer.

Allan Miller in a study of the feeding habits of *Morula,* found that *M. granulata* will prey on *Pomatoleios* (personal communication). However, *M. granulata* is most abundant in the upper intertidal areas on the exposed coast and it was not collected from the sheltered inshore areas where *Pomatoleios* was most abundant. Hence predation by *M. granulata* was probably marginal.

Although *Balanus* and *Ostrea* larvae settle least abundantly where *Pomatoleios* settle most abundantly, they, as well as vermetids, possibly compete for space with *Pomatoleios* after settlement. While *Balanus* attained a density of up to 1/10 sq mm in four weeks, it did not cause any observable mortality within the *Pomatoleios* population. *Ostrea* and vermetids were less abundant than *Balanus* and co-existed with *Pomatoleios* in the marginal areas of the *Pomatoleios* range. Following the green algal bloom in early August, *Balanus* and *Ostrea* mortality was 75% while no *Pomatoleios* mortality occurred on fouling plates.

Several species of colonial ascidians grew rapidly in the subtidal and lower intertidal areas. The level at which colonial ascidians were common rose from 0.1 feet below datum in July, to 0.1 feet above datum in August, to 0.4 feet above datum in September, to 0.6 feet above datum in October on horizontal fouling plates. On vertical surfaces, colonial ascidians only extended to 0.4 feet above datum in October.

A comparison of the area covered by colonial ascidians and *Pomatoleios* survival, shows that *Pomatoleios* survival decreases as the area covered by colonial ascidians

Table V

Pomatoleios *survival with increasing ascidian competition per 2 weeks*

Area occupied by ascidian (%)	*Pomatoleios* survival (%)
0–10	95–100
10–20	70
20–30	60–65
30–40	50
40–50	65
50–60	35
60–70	55
70–80	40
80–90	10–20
90–100	0

increases (Table V). Using the Spearman Rank Correlation Coefficient (Siegel, 1956), $r = -0.785$. This negative correlation is significant between 0.05 and 0.01 levels for a one tailed test. *Pomatoleios* mortality on the lower ten fouling plates (−0.5 to +0.6 feet) between July and the end of October (Fig. 3), was the result of competition from colonial ascidians.

As the effective sea level rose from July to October, the upper limit of the colonial ascidians rose and extended to the bottom of the *Pomatoleios* zone at C in October. Therefore during autumn, colonial ascidians compete for space with *Pomatoleios* that settled below the *Pomatoleios* zone during summer. Hence the lower level of the *Pomatoleios* zone at C was controlled by competition with colonial ascidians.

Discussion

Pomatoleios forms a narrow well-defined zone in sheltered intertidal areas. However, its survival range extends subtidally and the larval settlement range extends intertidally above the survival range during autumn and subtidally below the survival range during summer.

Lewis (1964, p. 217) states "it nevertheless appears from comparisons of many shores that wave action is primarily responsible for raising zonal boundaries, especially those of the upper shore where it is a matter of raising the theoretical height of the sea." While he was referring to localities exposed to different amounts of wave action, the present species shows a seasonal change in larval settlement height due to seasonal influence of the North Pacific Swell, trade winds, and changes in the predicted submergence at different levels. In this case, where the maximum tidal range is 3.0 feet, a shift in tidal levels of 0.4 to 0.6 feet effects a large portion of the intertidal environment. *Pomatoleios* settlement range changed seasonally as did the position of Min.H.W.S. (position that is submerged at least once a day) which is higher during autumn and spring than during summer and winter. In spring and autumn, most larvae settle within the *Pomatoleios* zone, while in summer, settlement is most abundant below the *Pomatoleios* zone. Settlement ceases during winter.

While the *Pomatoleios* settlement zone is higher on the shoreline in October than July, so is the distribution of algae and ascidians. The ascidians extend to the bottom of the *Pomatoleios* zone during October and kill specimens of *Pomatoleios* that settled below the *Pomatoleios* zone in summer. Algae extend into the lower *Pomatoleios* zone but do not affect specimens of *Pomatoleios* already present. However, continuous algal movement and accumulation of sand reduce larval settlement. Larvae which settle above the *Pomatoleios* zone during spring and autumn are reduced in numbers during summer and winter. They are attacked by crabs, exposed to air for long periods when the level of Min.H.W.S. falls, and are exposed to low salinities.

Connell (1961, p. 722) states that "the lower limit of distribution of intertidal organisms is mainly determined by the action of such biotic factors as competition for space or predation. The upper limit is probably more often set by physical factors." In *Pomatoleios,* while exposure to physical factors was important in limiting the upper level of the population, predation by crabs was also an important factor. No predation was recorded at lower intertidal levels where the population appeared to be limited entirely by seasonal competition for space with colonial ascidians.

Lewis (1964, p. 230) states "It is important, however, to appreciate that although larval discrimination is an important and perhaps necessary adaptation to zonation, it does not explain zonation." However, larval discrimination during settlement may be more important in the Serpulinae than in other groups of zone forming species. *Mercierella enigmatica,* another zone forming serpulid, is also known to aggregate during larval settlement (Straughan, unpublished). Both these serpulid species are able to build their tubes in any direction so that intraspecific competition for space is not as important as in species where shape and size are less variable, for example, barnacles and spirorbids. At high population densities, the former form unstable communities that are easily dislodged by wave action, while the latter space themselves out during settlement (Knight-Jones and Moyse, 1961). Hence aggregation during settlement is probably more important in building up a zone in the Serpulinae than in groups where intraspecific competition for space occurs at high population densities; it reinforces the effect of differential survival of the adults.

Velocity of waterflow over the substrate, type of exposed surface (texture light, and color), and angle at which the surface is exposed, are factors effecting settlement at all depths. The fact that larvae did not differentiate between the surface with large even pits and a smooth surface, but showed a definite preference for a rough surface, suggests that the latter was preferred because it enabled firmer tube attachment.

This work was carried out while the author was the holder of an American Association of University Women Fellowship. The author is grateful to the personnel of the Hawaii Institute of Marine Biology for assistance with the project, to Jim McVey for identifying the ascidian material, and to Dr. Ian Straughan for assistance with the manuscript.

Summary

Pomatoleios kraussii forms an intertidal zone which extends from 0.5 to 0.9 feet above datum in the sheltered areas of Kaneohe Bay. The settlement range which extends subtidally, is wider than the adult survival range which in turn is wider than the *Pomatoleios* zone. The settlement range moves up and down the shore corresponding to seasonal changes in the level of minimum High Water Springs. The *Pomatoleios* zone is limited at the top by exposure to air and predation, and at the bottom by competition for space. Habitat selection within the settlement zone is influenced by surface texture, surface angle, exposure to currents, presence of sand and algae. Competition for space with *Balanus, Ostrea,* and vermetids is largely eliminated by different larval settlement preferences in these species.

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